

ECOLOGICAL EFFECTS OF FIRE IN GREAT LAKES SAVANNAS AND PRAIRIES: LITERATURE REVIEW

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INTRODUCTION

The important ecological role that fire plays in many North American ecosystems is well documented. The southern Great Lake region of the United States is one example where fire, in combination with biogeoclimatic processes, shaped the presettlement occurrence and distribution of numerous ecosystems (Daubenmire 1968). Approximately 4,000-6,000 years ago when post-glacial climate conditions were relatively warm and dry (Cohen 2004) fire-maintained ecosystems like prairie, savanna, oak woodlands, wet meadows, and prairie fens occurred as large complexes in a broad prairie-forest transition zone that extended from northwest Minnesota into Michigan (Nuzzo 1986). A cooler, moister climate followed this warm dry period and these conditions favored the spread and establishment of mesic vegetation (Hotchkiss et al. 2007). However, the prairie-savanna ecosystems persisted across the landscape, partially as a result of Native American burning (Cohen 2004) that restricted woody vegetation encroachment and stimulated herbaceous growth (White 1983, Anderson 1990) and cyclical climates (Lytle 2005). More recently (last 200 years) fire suppression, urban sprawl, and land conversion for agriculture has caused the decline and loss of prairie-savanna ecosystems across this region.

The literature on effects of fire, both prescribed and wildfire, on world-wide ecosystems is abundant and diverse. This literature includes comprehensive treatises and reviews (e.g., Wright and Bailey 1982, Whelan 1995, Hardy and Arno 1996, Pyne et al. 1996, DeBano et al. 1998, Smith 2000, Arno and Allison-Bunnell 2002, Pyne 2004, among others), region-specific treatises (Wright and Bailey 1980, Wade et al. 1989, Walstad et al. 1990, Agee 1996, Bradstock et al. 2002, Cary et al. 2003), ecosystem-specific compilations (Johnson 1996, Biswell 1999, Conner et al. 2001, Friederici 2003, Schuler and McClain 2003, Sugihara et al. 2006), and thousands of individual articles too numerous to reference here. Literature specific to the Lake States is also well represented (Ahlgren 1960, Anderson 1998, Haines et al. 1970, Simard et al. 1983, Grimm 1984, Heikens and Robertson 1994, Clark 1990, Reich et al. 1990, Frehlich 1995, Zhang et al. 1999, Cardille and Ventura 2001, Cardille et al. 2001, He et al. 2002, Cleland et al. 2004, Gustafson et al. 2004, Schulte and Mladenoff 2005, among others).

However, many of the Lake State examples in the literature focus on forested ecosystems with less attention directed at prairies and savannas (except see the review by Heikens and Robertson 1994).

In the early 21st century, prairie and savanna ecosystems tend to occur as isolated, dysfunctional patches in the southern Great Lakes region. Within the region both prairies and oak savannas are recognized as communities in peril. For example, Michigan's Natural Features Inventory identifies several southern peninsula fire-dependent communities that are currently imperiled or critically imperiled ([MNFI](#)), and Wisconsin's Natural Heritage Program recognizes several grassland, savanna, and southern forest communities that are rare ([WDNR](#)).

Conservation efforts recognize that fire is an integral part of these ecosystems, but questions remain as to how prairie and savanna ecosystems respond to prescribed fire, particularly in the presence of contemporary land use issues and climate change. Prairie-savanna landscapes in the southern Lake States were dynamic, relying on large-scale repeated disturbance for diversity and stability (Taft 1997). With an increasing emphasis on prescribed burning as a management tool in the southern Lake States, discussions by state agencies on substituting other disturbances (e.g., mowing, grazing, herbicides) in place of fire to reduce liabilities and save money, and changing land use demands with potentially large-scale impacts on ecosystem dynamics (e.g., biofuels), we undertook this literature review to synthesize the knowledge on fire effects in the southern Great Lakes region and to identify topics that are in need of further research.

Prairie-Savanna Ecosystems

Numerous definitions have been proposed for the different fire-dependent ecosystems addressed in this literature review (see Nuzzo 1986, Heikens and Robertson 1994, Anderson 1998). We chose to emphasize broad categories of southern Great Lakes fire-dependent ecosystems. These ecosystems are extremely diverse and dynamic depending on fire regime, climate, topography, soil (Anderson 1983), and possibly browsing or grazing by herbivores (Nuzzo 1986). In fact, it is not uncommon for these ecosystems to mimic other rare ecosystem types depending on fire intensity and frequency (Nuzzo 1986), further complicating explicit definitions of individual ecosystems. To help organize our

literature review we categorized fire-dependent ecosystems into the general classes of prairie, savanna, fen, and wet meadow (Table 1).

Individually, prairie, savanna, fen and wet meadow ecosystems are often identified and mapped, particularly as remnants in highly modified landscapes, which tends to mask the importance of juxtaposition and interspersions on ecological functionality (Marks 1942). For example, the likelihood of fire maintaining the herbaceous-shrub structure of fens was highly dependent on juxtaposition to prairie and savanna types that more readily carried and propagated fire (Moran 1981). It is not uncommon for prairie, savanna, fen, and wet meadow ecosystems to occur as complexes in the southern Great Lakes region (e.g., Indiana Dunes National Lakeshore), with location of each individual ecosystem in the complex influenced by topography, micro-climate, soil characteristics, and fire regime (Ewing 1924, Marks 1942, Vogl 1964, Bacone and Post 1986, Brewer and Vankat 2004). In this review we refer to landscape mosaics of prairie, savanna, fen, and wet meadow ecosystems as “prairie-savanna ecosystems”.

Table 1. Ecosystems used throughout this document and brief description of distinguishing characteristics.

Community	Description
Prairie	Land of low topographic relief supporting grasses and forbs, with few trees
Savanna	Prairie-woodland mosaic vegetation type with spaced (i.e., broken canopy) trees (oak dominated) and an unbroken herbaceous layer
Fen	A wetland type fed by groundwater
Wet Meadow	Herbaceous dominated land saturated with water throughout much of the year

Literature Search

In conducting this literature review we focused on southern Great Lakes landscapes where fire was historically a dominant disturbance agent. Cleland et al.’s (2007) map of ecoregions and subregions of the United States formed the basis for ecoregion section descriptions, which were used to define the geographic boundary for the literature review.

In the southern Great Lake region we identified four ecoregion sections that historically contained fire-dependent prairies and savannas (Fig. 1). These ecoregion sections occur in the Midwest Broadleaf Forest Province (Cleland et al. 2007) in Michigan, Ohio, Indiana, Illinois, Wisconsin, Iowa, and Minnesota. We also included southeast Ontario in the literature review assuming that the South Central Great Lakes Section extended into this Canadian Province (Fig. 1).

Delineation of the study area purposefully avoided the well-studied prototypic tallgrass prairie ecosystems of the central United States (e.g., central Illinois, Iowa, Kansas) because these ecosystems are associated with a different ecological province (Prairie Parkland – Temperate) and disturbance-effects hypotheses (Peterson and Reich 2008). Tallgrass prairie ecosystems in the southern Great Lake region experience greater precipitation and may have evolved with a greater fire frequency and less intense grazing than tallgrass prairies in the central United States (Bowles and Jones 2013). Kline and Cottam (1979) found that fire in the driftless area of southwest Wisconsin burned in a patchy mosaic as influenced by topography and moisture (as opposed to a broad-scale, advancing fire front). Also, plant community composition in the southern Great Lakes prairie-savanna ecosystems may respond to fire consistent with the intermediate disturbance hypothesis (i.e., species richness is maximized at an intermediate level of disturbance frequency; Davis et al. 2005, Peterson and Reich 2008), which is different than patterns observed in the western range of tallgrass prairies (some prairies continue to increase in species richness up to decades after the last fire because woody encroachment is less aggressive and pervasive). Because of these differences we would not anticipate that the eastern tallgrass prairie ecosystems in the southern Great Lakes region would respond to fire in the same way as tallgrass prairie in the central United States.

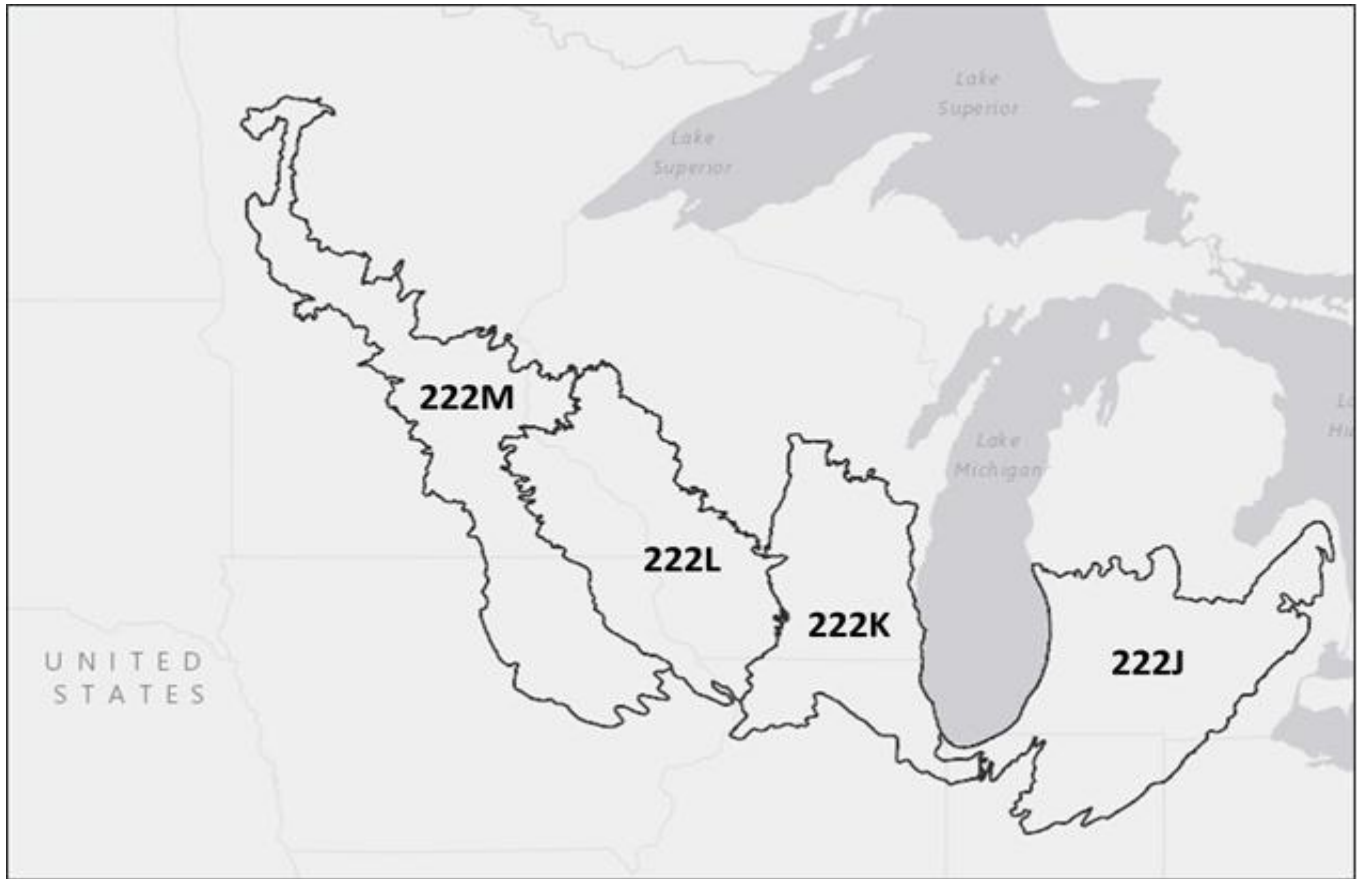


Figure 1. Map of ecoregion sections considered in this literature review, labeled with section codes. These sections include the Minnesota and Northeast Iowa Morainal Oak Savanna Section (222M), North Central U.S. Driftless Escarpment Section (222L), South Central Great Lakes Section (222J), and Southwestern Great Lakes Morainal Section (222K). All sections occur within the Midwest Broadleaf Forest Province (not outlined). Map created by T. Hmielowski using [Data Basin](#).

Electronic journal databases at Michigan State University and the University of Wisconsin at Madison libraries, and Google Scholar were queried for fire-related articles in the southern Great Lakes region. We also obtained a draft copy (Draft 9-02 Working Document) of a “Reference List and Annotated Bibliography of Natural Disturbance in the Lake States” by P. J. Anderson, D. T. Cleland, and J. C. Zasada with the USDA Forest Service, Northcentral Research Station that contained 500+ references. Other published bibliographies were also reviewed including Kirby et al. 1988, Henderson and Statz (1995), a United States Forest Service disturbance reference list (USFS), and a United States Geological Survey fire-amphibian reference list (USGS 2003). Research articles based on field experimentation were preferred and thus,

articles on modeling and describing historical disturbance regimes were treated as secondary sources of information.

SUMMARY OF INFORMATION

The majority of studies in prairie-savanna ecosystems of the southern Great Lake region have occurred in Minnesota and Wisconsin. These areas correspond to three of Cleland et al.’s (2007) ecoregion sections: 1) Minnesota and northeast Iowa morainal oak savanna, 2) north-central United States driftless and escarpment, and 3) southwestern Great Lakes morainal. These ecoregion sections were impacted by the latest glacial epoch and supported prairie-savanna ecosystems prior to European settlement (McNab and Avers 1994). The Minnesota

and northeast Iowa and southwestern Great Lakes morainal sections have similar topography as the result of glaciation, characterized as generally flat with some low hills (McNab and Avers 1994). In contrast, the north-central United States driftless and escarpment section has a topography characterized as a maturely dissected upland plateau with flat-bottomed drainages in the south and narrow, v-shaped drainages in the north (McNab and Avers 1994). Also, soils in the northern portion of the Minnesota and northeast Iowa morainal oak savanna tend to exhibit poorer drainage (McNab and Avers 1994) and occur on calcareous bedrock (Will-Wolf and Stearns 1998) compared to the other sections.

Comparatively few studies were identified for the south-central Great Lakes section. The south-central Great Lakes section was also impacted by glacial activity and historically supported prairie-savanna ecosystems, but differed from the other ecoregion sections by being more heavily influenced by oak-hickory invasions from the south (McNab and Avers 1994). We acknowledge the shortcomings of comparing results across studies due to definition differences (Anderson 1998) and variability in abiotic and biotic factors among ecoregion sections in the southern Great Lakes. Inference of specific study results to the entire southern Great Lakes region is risky, but there is knowledge to be gained in looking for repeatable patterns across studies.

The Biogeoclimatic Template

Middle Holocene to Present

It is tempting to attribute the decline in southern Great Lakes prairie-savanna ecosystems to a disrupted fire regime and land conversion, but one must also recognize that climate, topography, and hydrology also interact to influence ecological organization (Abrams 1992, Camill et al. 2003, Hotchkiss et al. 2007). Since the peak of prairie-savanna ecosystem distribution 4,000-6,000 years ago in the southern Great Lakes (Umbahowar et al. 2006), there have been large scale changes to the distribution and boundaries of prairie-savanna ecosystems. Sediment, charcoal, pollen and terrestrial carbon dating indicate that the latest woody species invasions into prairie ecosystems started about 5,000 years ago (Anderson 1998, Clark et al. 2001, Lytle 2005) with an increased abundance of oak (*Quercus* spp.), shrubs, and in some cases aspen (*Populus* spp.; Grimm 1983). At large spatial (e.g., ecoregions) and broad temporal (e.g.,

millennia) scales dynamics of this invasion were primarily determined by climate and its effects on vegetation and fire (Buell and Cantlon 1951, Clark 1989a, Anderson 1998, Umbahowar et al. 2006, Nelson et al. 2004, 2006). Woody advances into prairie ecosystems showed an uneven progression (McClain et al. 2006), with phases of rapid invasion separated by intervals with less or no invasion (Buell and Cantlon 1951). This periodicity was most likely climate driven (Buell and Cantlon 1951, Clark 1989a), with pulses of climatic conditions favoring woody species extension (i.e., cooler, moister) and changes in C₄ grass abundance (often at the expense of weedy species) becoming increasingly pronounced from 5,000 years to present (Nelson et al. 2004, 2006, Lytle 2005). General trends in vegetation composition suggest that C₄ plants are adapted to warm and dry climatic conditions, but not extreme droughts, and that the inherent fire regime of a landscape is controlled by biomass-climate interactions (Camill et al. 2003, Nelson et al. 2004).

At smaller spatial (e.g., 1,000's to 100's ha) and temporal (e.g., centuries to decades) scales topography and hydrology affect fire behavior and the patterns of woody invasion (Grimm 1983). Ewing (1924) and Bullington (1970) noted the importance of topography (particularly depressions) in providing favorable patches of hydrophytic and semi-hydrophytic conditions where woody vegetation succession occurs and radiates from. Counteracting invasion from woody refugia are well-drained soil areas (both clayey and coarse-textured) and areas supporting a dense herbaceous mat that restricted seedling establishment and tree growth (Ewing 1924, Bullington 1970, Lorimer 1993, McClain et al. 2007, but see Brown and Archer 1999). Depending on climatic conditions, fire acted on this physical template resulting in a landscape of inter-mixed prairie, forests (of varying tree species), and wetlands (Ewing 1924, Buell and Facey 1960, Kline and Cottam 1979). Fire by itself, however, could not completely deter the spread of woody invasion into Great Lakes prairie ecosystems. Droughty conditions also played a role in holding the prairie-forest border (Transeau 1935, Bullington 1970), but relatively cool moist climatic conditions over the last 1,000 years have favored mesic species establishment and spread resulting in documented prairie loss prior to European arrival (Grimm 1983, Grimm 1984, Gajewski et al. 1985).

The majority of non-anthropogenic fires in the southern Great Lakes region prior to European arrival were lightning induced during June, July, and August, particularly during the arid millennia 8,000-4,000 years before present. Storm patterns suggest that summer lightning fires were once common throughout central North America when climatic conditions were warm and dry (Komarek 1968). Current techniques do not allow identification of pre-European settlement fire type (i.e., natural versus anthropogenic), but it is reasonable to assume that a portion of summer fires (and occasionally other seasons) were lightning caused. The historical record also suggests that the persistence of prairie-savanna ecosystems in the absence of a warm, arid climate were fire dependent (Umbanhowar et al. 2006), presumably a result of Native American burning activity (Dorney and Dorney 1989). At the time of European settlement in the southern Great Lakes region (mid 1800's) prairie-savanna ecosystems covered millions of ha in the Midwest United States (Nuzzo 1986, Anderson 1998). The northern transition zone between prairie and forest ecosystems consisted of fire tolerant oaks and aspen groves (Buell and Cantlon 1951, Grimm 1984). Vegetation was most strongly correlated with the fire-probability pattern, which, as described above, was a function of both abiotic and biotic factors (Grimm 1984, Clark 1989b, Brawn 2006). However, the importance of fire in maintaining the transition zone varied north to south with climate having a greater effect in more northern regions (Buell and Cantlon 1951, Clark et al. 2001) and topography having a greater influence in the east (Leitner et al. 1991).

Following European settlement the prairie and oak savanna region was rapidly altered. European impacts on vegetation patterns and fire regimes in southern Great Lakes prairie-forest ecosystems are well-documented (Gajewski et al. 1985, Brawn 2006), and the Midwestern United States shows the greatest change from pre-settlement fire regimes (Nowacki and Abrams 2008). The fire suppression and land conversion activities in this region exacerbated an already climatically induced loss of prairie-savanna ecosystems (McAndrews 1968, Wolf 2004, Hotchkiss et al. 2007). Current prairie-savanna ecosystems in the southern Great Lakes region occur in an agriculture and urban matrix making them especially vulnerable to invasive species, fuel characteristics out of historical norms,

and patch isolation (Brewer and Vankat 2004, Wolf 2004, Asbjornsen et al. 2007, Grossman and Mladenoff 2007). Conservation of these rare ecosystems has been aided by federal and state supported programs that influence land use trends (e.g., the Conservation Reserve Enhancement Program (CREP), Landowner Incentive Program (LIP), Partners for Fish and Wildlife Program, and prescribed burning). A focal area of these programs is the maintenance and restoration of rare ecosystems and critical wildlife habitat on private lands. As a result, considerable areas in the southern Great Lakes region have been enrolled in management programs that often stress the use of fire (Anderson 1990, Copeland et al. 2002). Research has shown that even in heavily degraded sites the prairie-savanna ecosystem footprint is retained and can be recovered (Vogl 1964, Kline and Cottam 1979, Middleton 2002) but recovery may require management approaches beyond fire reintroduction, including mechanical canopy manipulation and herbicide (Nielsen et al. 2003).

Future Climatic Impacts

Given that prairie-savanna ecosystems in the southern Great Lakes region were heavily influenced by climate during the Holocene, it follows that rapid climate change predicted for the future will likely have profound effects on prairie-savanna conservation. Temperatures are predicted to increase and droughts may be more frequent and longer lasting (Overpeck et al. 1991, Clark et al. 2002, EPA 2013). Warming and drying conditions were historically conducive to the formation and persistence of prairie-savanna ecosystems and their corresponding fire regimes. Increased aridity and decades of drought as projected under climate change scenarios will likely result in less productive grasslands (Clark et al. 2002). Additionally, increased levels of atmospheric CO₂ may increase the growth and spread of woody species (Bond and Midgley 2000, 2012), further challenging conservation of prairie-savanna ecosystems. Considering that prairie-savanna ecosystems in the southern Great Lakes are highly fragmented and often embedded in human dominated landscapes that limit the broad-scale use of fire, the conditions resulting from a projected warmer and drier climate could result in rapid landscape alteration, potentially resulting in increased loss of biodiversity.

Fire Effects on Soil Nutrients, Hydrology, and Ecosystem processes

Prescribed fires can have both short- and long-term effects on soil nutrients. Immediately following fires, soil nutrient availability typically increases in frequently burned ecosystems (Wright and Bailey 1982). However, these increased levels quickly return to normal, in some cases one-year post fire (Scharenbroach et al. 2012). Repeated prescribed fires can have long-term effects on soil nutrients, including increased pH at sites burned frequently (Tester 1989) and, under a history of low severity prescribed fire, soils can contain higher levels of NO₃, dissolved organic nitrogen, and total N (Scharenbroach et al. 2012).

The impact of fire on ecosystem nutrient dynamics depends on the proportion of biomass and nutrients susceptible to combustion (Boerner 1982). Nutrient cycling in plant communities with abundant below ground biomass (e.g., eutrophic systems, wetlands, grasslands) are less affected by fire than those with abundant above ground biomass (e.g., oligotrophic systems, dry sand savannas; Boerner 1982, Bedford et al. 1999). Fire is important to prairie-savanna nutrient cycling because decomposition rates tend to be slow (Vogl 1974, Homan and Grigal 1997). Rainfall following fire events rapidly removes nutrients from ash into the soil, and the relatively high cation exchange capacity of prairie soils prevents appreciable leaching (Lloyd 1971). However, Boerner (1982) noted that nutrients mineralized by wildfire had little effect on species response or ecosystem recovery in temperate grassland ecosystems because most nutrient storage was below ground. Dijkstra et al. (2006) found that small-scale vegetation composition influences mineralization rates, with plots dominated by C4 grasses (that tend to be favored by burning) having less available nitrogen than tree dominated plots. Dijkstra et al. (2006) surmised that nitrogen mineralization rates were higher in tree dominated plots because of higher litter nitrogen concentration and labile soil pools but caution that their results should not be generalized pending further research.

The hydrology of prairie savanna ecosystems is influenced by woody encroachment, varying overstory tree density resulting from altered fire regimes, and surrounding land use (Asbjornsen et al. 2007). Asbjornsen et al. (2007) demonstrated that differences in transpiration rates between savanna and woodland vegetation architecture and species

composition resulted in a lower water table on sites not maintained by fire. Surrounding land use potentially confounds the relationships among transpiration rates, vegetation architecture, plant species composition, and fire regime. For example, large-scale row-crop agriculture potentially raises water tables thereby facilitating woody vegetation encroachment into prairie-savanna ecosystems that occur in agriculture-dominated landscapes (Asbjornsen et al. 2007). Prairie-savanna restoration projects should consider the potential for reestablishing favorable hydrologic conditions by targeting hydrologically isolated sites (e.g., hilltops) or by expanding areas around remnant sites (Asbjornsen et al. 2007).

The wetland components of prairie-savanna ecosystems (i.e., fens, wet meadows, marshes) tend to exhibit broad nutrient gradients. Plant species richness declines as nutrient availability increases beyond certain thresholds (often referred to as nutrient enrichment; Bedford et al. 1999). A large proportion of North American wetlands are identified as either phosphorous limited or co-limited by nitrogen and phosphorous, especially those occurring on organic soils (Bedford et al. 1999). Relationships among nutrient enrichment, wetland productivity, and species richness are not always consistent (Bedford et al. 1999). Bedford et al. (1999), in their thorough review of nutrient availability and plant diversity in temperate wetlands, noted that understanding nutrient effects on ecosystem productivity alone is probably not sufficient to predict plant species diversity. Nutrient information must be coupled with knowledge of ecosystem properties (e.g., geo-climatic factors, disturbance regimes) and individual species life history traits to improve predictive power. Management activities that occur as part of prescribed fire implementation can also influence soil conditions. For example, firebreaks created around wetlands alter hydrology, while excluding fire from wetlands can lead to an accumulation of organic matter (Bishop and Haas 2005).

Altering the fire regime in prairie-savanna ecosystems can also result in changes to how nutrients are mobilized. The extent to which nutrients stored as biomass are mobilized to inorganic material depends on burn intensity and duration (Boerner 1982, Brye et al. 2002, Tix et al. 2006). The combination of reduced vegetation cover, warmer soil temperatures, and mobilized nutrients

after burning, in combination with sufficient water, increases soil microbial activity can result in increased nutrient mineralization (e.g., nitrogen, Dijkstra et al. 2006, Tix et al. 2006). Brye et al. (2002) found that a 6-year burn interval in a Wisconsin tallgrass prairie restoration resulted in nutrient export similar to nutrient inputs from atmospheric wet deposition (also see similar findings in Dijkstra et al. 2006), but nutrient export exceeded inputs on a 3-year burn interval.

Carbon storage in prairie-savanna ecosystems is also influenced by fire frequency. Fire suppression in oak savannas has led to an estimated $1.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ of carbon accumulation, with most carbon stored in woody biomass (Tilman et al. 2000). Tilman et al. (2000) found that approximately 110 Mg/ha of carbon was stored in prairie-savanna ecosystems that experienced historical disturbance regimes, compared to about 220 Mg/ha in vegetation patches experiencing fire suppression. Blair (1997) found that tallgrass prairie subjected to periodic (compared to annual and unburned sites) burning exhibited enhanced aboveground net primary productivity, consistent with the transient maxima hypothesis (Seastedt and Knapp 1993). This hypothesis states that plant productivity increases because of transient releases (i.e., periodic burning) from light and nitrogen limitations that result from periods of no or too frequent burning. Blair's (1997) results indicate that non-equilibrium responses to multiple, variable resources (e.g., light, energy, minerals) are important aspects of prairie ecosystem dynamics.

RESEARCH NEEDS

Soil, hydrology, and ecosystem processes

- Effects of increased CO_2 on woody plant growth (Bond and Midgley 2000, 2012)
- Long term impacts of frequent, low severity, prescribed fire on soil nutrients and plant community composition (Scharenbroch et al. 2012)
- Effects of prescribed fire on carbon storage and carbon cycles in frequently burned prairie-savanna ecosystems (Tilman et al. 2000)

Vegetation

Vegetation in the southern Great Lakes region transitions (west to east) from prairie to savanna to mesic deciduous forest to pine hardwoods, corresponding to changing gradients in climate, soil texture, and fire frequency (McAndrews 1966). These factors interact to influence abiotic conditions and disturbance regimes. Perhaps the most documented and studied effects of altered fire regimes are small-scale (e.g., patch, stand, and micro-site) changes in vegetation composition and structure, particularly as related to fire exclusion (Keane et al. 2002). In addition to fire exclusion the current landscape has been influenced by cultivation, agricultural abandonment, and topography (Homann and Grigal 1997). At small scales, research indicates that site factors and disturbance regimes are important determinants of ecological community composition and persistence (Bray 1960, Buell and Facey 1960, Leitner et al. 1991, Weiher and Howe 2003), though some argue that with disruption of historical disturbance regimes vegetation composition may simply be dictated by individual responses to chance events (McCune and Cottam 1985, Tester 1996).

The literature unequivocally recognizes the importance of a fire regime in maintaining vegetation structure of prairie-savanna ecosystems (Curtis 1959, Buell and Buell 1959, White 1965, Vogl 1969, Davis 1979, Anderson and Brown 1983, White 1983, McCune and Cottam 1985, Feist et al. 2004, Wolf 2006, McClain et al. 2006, 2007). Under historical disturbance regimes (which also included hydrological dynamics for the fen and wet meadow ecosystems) fires perpetuated herbaceous dominance in the understory and favored fire-tolerant tree species (i.e., oaks; White 1983, Abrams 1992, McClain et al. 2006). Disruption of the disturbance regime can result in significant changes to plant community structure and species composition over short time frames (i.e., 10-20 years; White 1983, McCune and Cottam 1985, Abrams 1992, Bowles et al. 2003).

Savanna tree component

Within prairie-savanna ecosystems, oak species assemblages and spatial distribution are partially determined by site conditions. The black oak group (subgenus *Erythrobalanus*) tends to occur on low-nutrient, well-drained sandy soils in a clumped, large patch distribution (Bray 1960, Rodgers and

Anderson 1979, Adams and Anderson 1980, Bacone and Post 1986, Will-Wolf and Stearns 1998). In contrast, the white oak group (subgenus *Lepidobalanus*) tends to occur as scattered single trees or small groves on well-drained soils with moderate nutrient status (Bray 1960, Rodgers and Anderson 1979, Will-Wolf and Stearns 1998). Tree clumpiness is often dictated by competition (reduces clumping) and disturbance, which at low and intermediate frequencies, tends to increase clumpiness (Davis et al. 2005). In some instances white and black oak co-occurred, with one species being dominant (e.g., Rodgers and Anderson 1979, Brewer and Vankat 2004), presumably a reflection of changing climatic and disturbance conditions (Wolf 2006). Both oak groups can succeed into bur oak (*Q. macrocarpa*) in southern Great Lakes savannas (Will-Wolf Stearns 1998), and bur oak is one of the common prairie-savanna ecosystem indicator species in this region (Cottam 1949, McClain et al. 1993, Anderson 1998, LaGesse et al. 1998, Peterson and Reich 2001, Wolf 2006). A recurring fire event (every 4-6 years) is important to maintain the bur oak savanna vegetation structure (Wolf 2006).

Most upland oak species exhibit physiological adaptations that facilitate survival on sites exposed to periodic fire and drought (Anderson and Brown 1983, 1986, Abrams 1992). The prototypic fire tolerant species in the southern Great Lakes region is bur oak because frequent fire does not appear to cause significant mortality in natural regeneration (Peterson and Reich 2001). Trees with fire adaptations often have deep roots, thick bark, sprouting ability, resistance to rot after scarring, xeromorphic leaves, low water potential threshold for stomatal closure, an ability to adjust osmotically, maintenance of high photosynthesis rates, favored propagation on fire-created seedbeds, and an ability to survive on nutrient poor sites (Reich and Hinckley 1980, Lorimer 1985, Abrams 1990, Kruger 1992, Krueger and Reich 1997a, 1997b, Collada and Haney 1998). Periodic fire is critical for stabilizing the overstories of prairie-savanna ecosystems (Anderson and Brown 1983, 1986). Fire return intervals significantly longer than normal result in unnatural fuel accumulations and burn severities, producing unnatural levels of overstory tree mortality (Anderson and Brown 1983, 1986).

A compounding factor in understating vegetation response to changing fire regimes is

climate. In fire-dependent ecosystems, episodic drought can play an important role in determining tree species composition (Transeau 1935, Faber-Langendoen and Tester 1993). For example, Faber-Langendoen and Tester (1993) found that bur oak was more drought resistant than pin oak (*Q. ellipsoidalis*) and contended that differential drought response among species was critical in maintaining certain species assemblages. Bur oak savannas tend to experience frequent droughts and fires and as a result, tend to be all-aged (Frehlich et al. 1992). More mesic pin oak woodlands tend to have less frequent but more intense fires, resulting in more even-aged stands that resulted from pulses in recruitment (Frehlich et al. 1992). Fire seems to be more important in determining plant community structure on mesic savanna sites than on savannas with poorer soils, suggesting that droughty conditions also play an important role in structuring savanna communities on poor soil types (Abrams 1992, Meisel et al. 2002). Episodic climate events affecting moisture can kill well-established oaks, depending on stand structure with closed savanna woodlands having lower mortality rates than open savannas (Faber-Langendoen and Tester 1993).

Additional disturbances that can influence stand structure on prairie-savanna ecosystems include herbivory, insect defoliations, grazing, and tree removal for timber. Herbivory and insect defoliation can have significant long-term effects on overstory species composition (Howe and Brown 2000, Howe and Lane 2004, Sekura et al. 2005). For example, Sekura et al. (2005) found that gypsy moth defoliation of oak seedlings significantly altered regenerating tree species dominance over a relatively brief (4 years) period. Likewise, voles can significantly alter species composition in wet-prairie ecosystems (Howe and Brown 2000, Howe and Lane 2004). Savanna trees can be affected by grazing that alters fire regimes, and selective tree harvesting that creates canopy gaps influences tree recruitment (Considine et al. 2013). These disturbances can have direct effects on prairie-savanna ecosystem vegetation architecture and species composition in that overstory trees are damaged or killed, and indirect effects caused by how these factors interact with fire. Hence, disturbance factors other than the direct effects of the fire regime should be considered when investigating the role of fire in re-establishing plant community structure.

Savanna understory component

In southern Great Lakes ecosystems subjected to maintenance fire regimes, woody understory vegetation is lacking, sparse, or isolated to fire resistant areas (White 1983, Kruger and Reich 1997b, Brawn 2006, McClain et al. 2007, Peterson et al. 2007, Peterson and Reich 2008), if the fires burn with sufficient intensity and frequency (Nielsen et al. 2003, Peterson et al. 2007). McCune and Cottam (1985) noted that understory species in the absence of fire originates from three sources: 1) expansion of species from their normal habitats, 2) colonization by invasive exotic species, and 3) increased abundances of less tolerant native species that were common, but historically not dominant. Savanna ecosystems not maintained by fire regimes contain a diversity of fire intolerant shrubs and tree regeneration (White 1983, Taft 2005, Brudvig and Asbjornsen 2007).

The compositional dynamics of savanna understories are individualistic in time and space, influenced partly by seasonal, aestival, and serotinal properties of the plants (Ewing 1924, McCune and Cottam 1985). A unique savanna understory association may not exist. Rather, savanna understory species composition appears intermediate to prairie and forest communities with few common geographic boundaries (though some species reach range limits; Curtis 1959, Bray 1960, Leach 1996, Anderson 1998). The understory successional trajectory of savanna and woodland ecosystems is more determined by chance events (e.g., disease, windthrow, introduction of exotics) and landscape context as opposed to some predictable successional sequence based on current woody species assemblages (Bray 1960, McCune and Cottam 1985).

Prairie, savanna, fen, and wet meadow ground layers

Surprisingly little is known about the composition, structure, and horizontal patterning of species rich ground layers in prairie-savanna ecosystems at small scales (Leach and Givnish 1999, Meisel et al. 2002). Ground layer composition is strongly related to fire regime (Nuzzo et al. 1996, Collada and Haney 1998, Howe 2000, Kost and De Steven 2000, Bowles et al. 2003, Nielsen et al. 2003, Johansson and Reich 2005, Taft 2005, McClain et al. 2007), climate (Clark et al. 2002), and to soil texture and light availability. Savannas tend to be forb-

dominated and diverse on partially shaded areas and graminoid dominated on the sunniest and driest sites (Leach and Givnish 1999, Meisel et al. 2002, Peterson et al. 2007, Peterson and Reich 2008). Forbs and perennial sedges often respond favorably to burning (Taft 2005). In fact, sedges rivaled grasses in diversity and abundance in some prairie-savanna ecosystems (depending on differences in geology and climate; Hipp 2007), likely accounting for 4-7% of the ground layer diversity (DeLong and Hooper 1996). In the absence of fire, sedges or alien grasses can become dominant, persistent members in savanna plant communities (Howe 2000, Bowles et al. 2003, Nielsen et al. 2003). Burning decreases ground layer vegetation cover and litter often resulting in increased herbaceous species diversity (Curtis and Partch 1948, Tester 1965, Nuzzo et al. 1996, Howe 2000, Bowles et al. 2003, Nielsen et al. 2003, McClain et al. 2005). Burning can also result in favorable conditions for rare plants (e.g., Bacone and Post 1986).

Prescribed burning programs need to consider population-level responses of plant species already occupying proposed treatment sites to be effective. This observation is particularly relevant for prairie-savanna restoration projects when invasive or exotic species control or eradication is a management objective. Burning has been documented as an effective control technique for some undesirable plant species (e.g., *Alliaria petiolata*, Nuzzo et al. 1996; *Phalaris arundinacea*, Howe 2000; also see Bowles et al. 2003, McClain et al. 2005). Suding and Gross (2006) found that native and exotic species richness were positively correlated and that the relationship could be skewed to favor native species by using fire in combination with native seed planting (also see MacDonald et al. 2007). Invasive or exotic species may have life history traits or fire responses completely different than native species and therefore require management approaches different from those commonly employed (e.g., summer burning, Howe 2000, Emery and Gross 2005; addition of native seed, Suding and Gross 2006).

Fire affects on the wet ecosystem (i.e., prairie fens, wet meadows) in the prairie-savanna landscape indicate that periodic fire with a recovery interval (2 years minimum) may best maintain desired plant diversity (Bowles et al. 1996, Kost and De Steven 2000). Vegetation response to fire is often immediate (one year after burning) and dramatic

(Warners 1987, Kost and De Steven 2000). Generally periodic burns have limited effect on overall community dominance by grasses and sedges in wet meadows (Warners 1987, Kost and De Steven 2000), can enhance seed production and viability (Apfelbaum et al. 1989, Kost and De Steven 2000), and can favor annual forbs (Kost and De Steven 2000, Middleton 2002). For example, Kost and De Steven (2000) found that more frequent fires reduced litter thereby stimulating annual forb growth.

In a prairie ecosystem, Henderson (1992) demonstrated that early flowering forbs persisted under a late-spring burning regime, indicating that plant susceptibility is at least partially attributed to seasonal phenology (Lovell et al. 1982, Hulbert 1988, Copeland et al. 2002). In contrast, Warners (1987) witnessed a short-term (1-2 years) decline in forb occurrences after a burn but their study occurred in a wetter, more shrub-infested ecosystem. Even in these wetter ecosystems, fire can favorably influence woody species composition (Warners 1987) but the objective of maintaining open conditions may be unattainable (Bowles et al. 1996, Kost and De Steven 2000, Middleton 2002).

As with the tree and understory components of prairie-savanna ecosystems, multiple factors influence ground layer vegetation response to fire, including starting species composition, soil moisture and nutrient availability, climate, fire intensity, and individual life history strategies. Prairie vegetation, similar to the tree component of savanna ecosystems, exhibits greatest large-scale responses to drought and fire frequency, with the drought-fire interaction being most influential (Henderson 1992).

Vegetation Response to Fire Regime and Fire Alternatives

The increased diversity of grassland herbaceous vegetation is a prescribed fire effect commonly documented by researchers in the southern Great Lakes region. Curtis and Partch (1948) found that prescribed burning allowed planted prairie grasses a chance to compete, spread, and grow in dense sod of old field quackgrass (*Elytrigia repens*) and bluegrass (*Poa* spp.), through the reduction of quackgrass and bluegrass cover and litter. This increased the diversity of herbaceous vegetation in a planted prairie in Wisconsin (Curtis and Partch 1948). Under current prescribed fire programs, prairie-savanna

ecosystems are burned in spring and fall, often corresponding to high moisture periods in wetland types and poor burn performance except during drought years (Cole et al. 1992, Battle and Golladay 2003, Bishop and Haas 2005). In contrast, vegetation responses to summer fires in wetland types can be dramatic, with entire shifts in plant and animal community responses (Laubhan 1995).

The recurring theme among studies on vegetation responses to burn timing is that season is a critical determinant of resulting vegetation community structure and composition. With seasonal changes there are shifts in plant development stage, and soil and surface moistures, all of which are critical determinants of fire intensity and fire effects. To truly understand fire effects in prairie-savanna ecosystems one must know pre-burn vegetation composition and density and understand factors causing variation in fire intensities (Cole et al. 1992). Individualistic plant adaptations to fire and other disturbances will influence the resultant community and fire managers are encouraged to align time of burn with resultant plant community objectives (Cook 2000). Management practices that strongly favor dominant graminoids (like early spring or late fall burns) can have negative consequences for competitively inferior subdominants (Copeland et al. 2002), potentially undermining long-term maintenance of diverse prairie-savanna ecosystems (Howe 1994, Howe 1999a, 1999b). Plant community expression to fire is partly determined by the interaction between fire timing and plant development stage, individual plant adaptations, and changes to the physical environment that change competitive relationships (Copeland et al. 2002). Characteristic fire temperature profiles serve to perpetuate certain communities and deviations from these profiles can lead to shifts in floristics (Cole et al. 1992).

The challenge is to create or maintain prairie-savanna ecosystems in a manner that supports enough common dominants to provide the intended overall community structure without inadvertently eliminating floral diversity or facilitating undesirable weedy encroachment (Copeland et al. 2002). In southern Great Lakes prairie-savanna ecosystems late summer (September) prescribed fires have been shown to increase the frequency and richness of subdominant species (Copeland et al. 2002), and late spring burns to decrease species density and diversity (Henderson 1992). These results are

presumably because these burn seasons corresponded to important development stages of subdominant species (Robocker and Miller 1955, Henderson 1992, Copeland et al. 2002). When considering conservation or restoration of prairie-savanna ecosystems, these findings reinforce the importance of understanding individual plant response to fire and making sure community structure objectives include those considerations (Howe 1994, Howe 1999a, 1999b).

Floristic responses to fire vary by ecosystem type and fire intensity (Tester 1989, Cole et al. 1992). Frequently occurring (annual), low intensity spring fires had minimal effects on oak survival, growth, and ecophysiology in mesic savannas (Kruger 1992). These effects increase with fire intensity, as tree mortality rates directly relate to soil temperatures near root collars (Johnson 1974). In subsequent years after a fire occurs, oaks exhibit significant physiological responses (Reich et al. 1990). Low intensity spring burns can result in woody understory increases (e.g., hazel (*Corylus* spp.; Axelrod and Irving 1978, Alleghany blackberry (*Rubus allegheniensis*; Reich et al. 1990) and, in situations where oak regeneration is desired can have minimal impact on competing woody and herbaceous vegetation (Johnson 1974, White 1983, Cole et al. 1992).

Rest intervals between fires that permit replenishment of seed banks, especially for transient species may be important (Kucera and Koelling 1964, Kost and De Steven 2000). Some researchers contend that ≥ 4 fires per decade in savanna ecosystems cause excessive sapling mortality and may result in unsustainable oak populations (Peterson and Reich 2001). Peterson and Reich (2008) found that understory vascular plant species richness was greatest for sites managed with biennial fire frequencies. Biennial fire frequencies appeared to promote high forb cover, species richness, and spatial heterogeneity (Peterson and Reich 2008). Less frequent fire frequencies resulted in high tree cover and simplified woody understories, whereas annually occurring fires tended to favor abundant C₄ grasses, some persistent woody sprouters, and some common prairie forbs (Peterson and Reich 2008). Burn results are quickly lost (5-7 years) in herbaceous dominated ecosystems (Kucera and Koelling 1964, Kost and De Steven 2000, Peterson and Reich 2001).

Few studies have determined how fire behavior influences vegetation response. Cole et al. (1992) measured fire temperature during prescribed fires in a mosaic of mesic and wet prairies and oak savanna and mesic oak woods in Indiana. Temperatures varied within and among vegetation types (Cole et al. 1992). Significant differences between above and belowground burn temperatures and flame lengths between vegetation types were attributed to the climate, topography, and the fuel loads and hydrology of the vegetation types (Cole et al. 1992). Although the highest aboveground burn temperatures were in the prairie vegetation types, the highest soil temperatures were in the mesic oak woods (Cole et al. 1992). Cole et al. (1992) also examined the effects of fire temperatures on trees, which were found to correlate with fire temperature and tree diameter; smaller trees had higher percent mortality, which increased with temperature. However, larger trees had low mortality, even at high temperatures (1300 °C; Cole et al. 1992). These results indicate that many of the abiotic and biotic effects of prescribed fire will depend on site-specific characteristics, which will vary among vegetation types and structure, topography, hydrology, and fuel loads.

Restrictions on burning have led some restoration ecologists to explore other vegetation management approaches. Fire effects on ground layer vegetation, particularly species composition, are difficult to replicate with mowing, grazing, or mechanical thinning. Brudvig and Asbjornsen (2007) found that mechanically treated white oak savannas were quickly repopulated by woody shrub sprouts and tree regeneration. They suggested that woody encroached savannas potentially act as an alternative steady state, suggesting that a relatively severe disturbance is necessary to shift states (for example, shift back to a savanna understory dominated by herbaceous species). Tix and Charvat (2005) tested a combination of mowing and raking (for litter removal and light scarification) for maintaining prairie species assemblages. They found that raking helped emulate fire effects, but burning tended to reduce C₃ forbs and grasses and increase C₄ grasses more extensively than mowing and raking.

RESEARCH NEEDS

Vegetation

- How fire behavior (e.g., fireline intensity, temperature) impacts vegetation structure and composition (Cole et al. 1992)
- Influence of season of burn on vegetation composition and structure, particularly response of species to seasonal timing (Henderson 1992, Copeland et al. 2002)
- How additional fuel manipulation techniques (e.g., mechanical, herbicide, grazing) interact with prescribed fire (Tix and Charvat 2005, Brudvig and Asbjornsen 2007)

Animal Responses to Fire

Animal communities associated with the central United States oak savannas and woodlands are species rich but composed mostly of species that have distribution centers in deciduous forests to the east or in the prairie biome to the west (Temple 1998, Grundel and Pavlovic 2007). A recurring theme among studies that explored animal community responses to fire is that responses are species-specific. Species tend to show individualistic adaptations to particular habitat types within the prairie-savanna mosaic (Temple 1998).

Fire effects on animal communities can be categorized as direct and indirect. Direct effects are defined as those where one variable (i.e., fire) has an affect on another variable (e.g., heat induced mortality, suffocation, a repellent effect on behavior) via a single causal path. Indirect effects are those in which the relationship has intermediary affects (e.g., fire alters vegetation and vegetation loss causes a reduction in animal survival). Warren et al. (1987:107) characterized direct effects as acute (that occur during burn combustion and “shock” phases) and chronic (plant community recovery phase and resultant state).

Arthropods

Arthropod responses to fire depend on taxonomic class, genera, and species-specific life history traits. Plant community characteristics interact with environmental conditions at burn time

to determine the acute effects of fire on arthropods (Warren et al. 1987). Arthropod habitat use often associates with small-scale features found within plant communities (e.g., a host-plant patch, wet microsites; Haysom and Coulson 1998) and responses to these features are determined by specific adaptations or life history strategies. The tremendous species diversity in phylum Arthropoda and potential for rapid population response makes generalizations on the effects of fire difficult (Swengel 2001). Detailed reviews on this topic have been compiled (Warren et al. 1987, Swengel 2001) and the intent is to not reproduce those documents here. Rather, we summarize the general patterns that emerged from fire-arthropod studies in the southern Great Lakes region (and other pertinent studies).

The life history cycles of arthropods can determine their vulnerability to fire. For example, fire is detrimental to different species of mites and ticks (Subclass Acari) if timed to the host-seeking life cycle stage (particularly for the “hard ticks” [Ixodidae]). In contrast, burning can have little lasting effect on subterranean or detrital arthropods (e.g., springtails [Order Collembola]; Lussenhop 1976, 1981, Kalisz and Powell 2000) because their life history strategies shelter them from direct fire effects (see Brand 2002 for conflicting results). Adding to the complexity of population responses are variations in fire intensity, coverage, plant community recovery stage, and how host plant species are used as habitat (Warren et al. 1987).

Fire effects on the environment are highly variable (Anderson et al. 1989), and describing arthropod responses is confounded by potentially obscure differences in plant communities among studies. This observation partially explains seemingly contradictory results. For example, Lussenhop (1976, 1981) found little lasting effect of a spring burn in Wisconsin on springtails, but van Amburg et al. (1981) documented a slow decline in springtail populations 45 days after burning in a Minnesota prairie. These results are probably linked to differences in soil temperature and moisture regimes at various stages of plant community recovery (van Amburg et al. 1981, Seastedt 1984b), which have been shown to influence arthropod hatching (Knutson and Campbell 1976, Evans 1984). Brand (2002) found that springtail populations on unburned areas over a 12-year period exhibited greater species richness, frequency of occurrence, and densities when compared to burned

areas in bur oak-white oak-red oak woodlands. Brand (2002) recommended a fire return interval of 2-3 years to help alleviate the negative consequences of burning on springtail populations.

The fragmentation of habitat patches also raises concerns about localized population loss for arthropods following fire. Many arthropod species exhibit a predictable population response to fire (Rice 1932, Tester and Marshall 1961, Bulan and Barrett 1971; Riechert and Reeder 1972; van Amburg et al. 1981, Seastedt 1984b, Anderson et al. 1989, Harper et al. 2000, Kalisz and Powell 2000, Swengel 2001). Populations tend to decline markedly over the short-term (immediately through 1-2 months), followed by rapid (weeks to months) recovery of predominately generalist species, followed by slower or in some cases no recovery of specialist species (Swengel 2001, Panzer 2002). Arthropod community recovery rates and composition associate closely with plant, environment, and prey dynamics following a fire. For example, predatory arthropod species (e.g., wasps, spiders, centipedes, some beetles, some grasshoppers) may be initially attracted to burns (because of large number of fleeing and disrupted prey; Komarek 1970, Gillon 1972), followed by a short-term reduction corresponding to lack of prey (Rice 1932, Tester and Marshall 1961, Nagel 1973, Seastedt 1984b), and further followed by a subsequent increase as prey populations recover (van Amburg et al. 1981). In addition to causing short-term population reductions, burning may constrain arthropod population growth by reducing available producer energy and creating more xeric habitat conditions (Bulan and Barrett 1971).

Short-term post-fire arthropod population declines are often related to flame exposure. Species occurring underground, within or beneath unburned debris, above flames in treetops, or highly mobile are observed to have lesser declines (Swengel 2001). Most evidence for immediate fire mortality is implied because many arthropods, especially smaller ones or immature stages, become minuscule and unrecognizable in ash (Swengel 2001). The recovery of Arthropod populations can be rapid following fire, but decreased species richness can persist for longer time periods. For example, Riechert and Reeder (1972) found that large numbers of surface-dwelling spiders (Subclass Araneae) were eliminated by spring burning in a southwest Wisconsin prairie (also see results in Rice 1932 on mites from Illinois).

The community recovered within a week, but was dominated by vagrant species. Species composition eventually recovered to pre-burn conditions, but well into the recovery phase of the plant community (Warren et al. 1987). This same pattern in arthropod population response was also observed for grasshoppers in Kansas tallgrass prairie (Evans 1984, 1988). Anderson et al. (1989) noted that burning does not necessarily generate strong patterns in grasshopper communities but rather it sets broad limits on species composition.

Some arthropod groups exhibit benign or favorable short-term population responses to fire. Favorable or benign responses have been observed for some beetles, millipedes, springtails, true bugs (Order Hemiptera), homopterans, and mites (Rice 1932, Cancelado and Yonke 1970, Lussenhop 1976, 1981, van Amburg et al. 1981, Harper et al. 2000). During or immediately following combustion some arthropods can be attracted to heat, flame, or smoke as a focal point for mating, predation, or egg-laying (Komarek 1970, Evans 1972, reviewed by Swengel 2001). Favorable population responses can also be attributed to luxuriant plant regrowth on burned areas, particularly for those species depending on aboveground plant productivity or on life history strategies that have specifically evolved to survive fire and exploit conditions resulting from the burn. For example, some species of ants increase following burning because of their cryptic habits (that let them survive the fire), their tolerance of dry soil, and social habits that are conducive to rapid recolonization (Ahlgren 1974, Warren et al. 1987). Generalist grassland species tend to dominate burned areas. Specialist species occurrence is related to plant community recovery, specifically the re-appearance of certain plant species or vegetation architecture (Swengel 2001). In general, short-term post-fire environments favor arthropods that depend on sunny, xeric, grassy conditions but disfavor or eliminate species requiring shade, moisture, and diverse flora (Swengel 2001).

The long-term effects of repeated burning both negatively and positively impact arthropods in prairie and oak savanna ecosystems. Some above ground arthropods residing in plant communities subjected to repeated burning may not readily recover to pre-burn levels (Rice 1932, Seastedt 1984a, Swengel 1996, Swengel 2001, Vogel et al. 2010) until the plant community is left undisturbed for an extended time (years to decades; Johnson

1995, Siemann et al. 1997, Swengel and Swengel 2007). This observation is particularly relevant for species with specific floristic or vegetation architecture habitat requirements that take time to develop (Swengel 1996). For example, butterflies and moths (Order Lepidoptera), particularly specialists of native prairie-savanna ecosystem flora, have shown longer-lasting post-fire population effects (Swengel 1996, Swengel and Swengel 1997a, Swengel 1998). Frequent fires might preclude these critical resources from ever recovering thereby restricting arthropod community diversity, known as the "fire attrition hypothesis" (Panzer and Schwartz 2000). Panzer and Schwartz (2000) found little empirical evidence in support of the fire attrition hypothesis, in fact, in other instances, arthropod communities (prairie and wetland butterflies, moths, and leafhoppers) exhibit greater species richness in frequently (≤ 5 years) burned habitats (Panzer 1988). These conflicting results present a conundrum for conservation biologists and fire managers. Prescribed fire, which must be conducted under controllable conditions, often requires frequent repeated application to achieve and maintain plant community objectives. Some arthropod species are negatively affected by this management regime (Panzer 2002). In contrast, wildfire tends to burn hotter and more expansive but less frequently. Thus, a wildfire regime is beneficial to those species that depend on the vegetation or prey assemblages resulting from less frequent fire occurrence (Swengel 2001).

Arthropod community response to different fire regimes depends on a combination of species dispersal capabilities and landscape context. The interactions between fire return interval, arthropod species dispersal and landscape context have led several researchers to advocate for networks of unburned refugia as source habitats (Panzer 1988, Anderson et al. 1989, Brand 2002). Arthropod species richness increases with patch area, consistent with island biogeography theory (Panzer and Schwartz 2000). Research has demonstrated that arthropods restricted to prairie-savanna ecosystems (particularly butterflies, see list in Panzer 1988:84-85, Swengel 1996, Panzer 2002) are susceptible to extinction because their populations fluctuate, they have poor dispersal capabilities, and their habitats are patchily distributed (Panzer 1988, Panzer 2002). Source patches should be relatively close (3-5 km; Swengel and Swengel 1997a, King 1998), of the

same ecosystem type, and capture the range of spatiotemporal variability in plant community development (Swengel 2001). Swengel (2001) cautioned that losing spatiotemporal variability leads to plant community uniformity and niche loss among sites of the same ecosystem type.

Arthropod population responses to different vegetation management approaches that are intended to replace fire have also been evaluated. All management approaches disrupt existing habitat structure thereby resulting in short-term changes to the arthropod community. However, differences in magnitude of population responses have been documented. As with fire, season and scale of vegetation manipulation effect which species populations respond and in what direction (Swengel 2001). Arthropod declines (particularly for above-ground insects) immediately following mowing are less severe and shorter in duration than declines observed after fires of comparable timing and size (Swengel 1996, Swengel 2001). Light grazing can emulate mowing, but heavy grazing increases niche simplification to the point that arthropod population responses mimic intense fires (i.e., a few species respond favorably [e.g., grasshoppers, Joern 2004], but more respond negatively, Swengel 2001). Study results on arthropod population responses to different management approaches indicate that one management type will not be most appropriate for an ecosystem composed of numerous arthropod habitats. Type, timing, and spatial extent of management depend on the species being considered and the region and landscape context of treated sites (Swengel 2001). It is difficult to holistically justify the investment in fire management or substantiate harm from it because arthropods exhibit varied species-specific responses (Swengel 2001). Clearer direction emerges when individual species conservation is considered (e.g., Karner blue butterfly (*Lycaeides melissa samuelis*) but even then differences may be minor (Swengel and Swengel 1997b, Swengel 2001).

An underlying assumption of using fire for arthropod conservation in southern Great Lakes prairie-savanna ecosystems is that most habitat-restricted species will be best adapted to the ecological forces historically prevalent in the ecosystems (Evans 1984, Anderson et al. 1989, Swengel 2001). This assumption is somewhat refuted by the fact that distribution and abundance of several open-habitat arthropods can persist in the

long-term absence of fire (Swengel 2001). For example, Swengel and Swengel (1997b) found that specialist butterflies occurred at lower species richness and densities on burned sites than on hayed, grazed, or mowed sites, even though the burned areas were viewed as ecologically restored because of fire management. Panzer et al. (1995) found that <25% of prairie-savanna inhabiting insects in northern Illinois were remnant dependent. Available data suggest that arthropods persisting in fire (and other disturbed landscapes) do not necessarily exhibit unique fire adaptations, *per se*. Rather, their ability to persist depends on biological mechanisms and traits that are consistent among taxonomic groups (as opposed to consistent among ecosystems, Swengel 2001). For example, subterranean pupal locations exhibited by arthropod taxa worldwide undoubtedly afford protection in fire maintained ecosystems but this life history trait does not indicate co-evolution specifically with fire but probably a variety of different disturbance types (Frost 1984, Hardwick 1996).

RESEARCH NEEDS

Arthropods

- Multi-year, multi-site studies that look at insect community response as a whole (Panzer 2002)
- Effects of non-fire management techniques (e.g., grazing, mowing) to maintain open habitat for wide range of insects (Swengle 2001)
- Effectiveness of refugia within isolated patches

Amphibians and Reptiles

Few studies have examined the effects of fire on amphibians or reptiles. Most studies are observational with few based on an experimental designs that explore different fire regimes over long time periods. Forces influencing broad-scale species distributions in southern Great Lakes areas (e.g., Illinois) differ between reptiles and amphibians, with reptiles more closely associated to broad-scale climate and vegetation (which also represent inherent ecosystem disturbance regimes) and amphibians more closely associated with drainage

patterns (Bock et al. 1981). In general, a paucity of information exists on amphibian and reptile responses to fire in the southern Great Lakes region.

Several reviews on fire-amphibian relationships have been completed (Means and Campbell 1981, Russell et al. 1999, Parr and Chown 2003, Pilliod et al. 2003, also see USGS 2003), but literature specific to the southern Great Lakes region is non-existent. This is somewhat surprising given that amphibians associated with prairie-savanna ecosystems (e.g., Blanchard's cricket frog [*Acris crepitans blanchardi*]) are recognized as species of concern throughout this region (also see Brodman et al. 2002). Even outside of the southern Great Lakes region, fire-amphibian studies have focused on short-term (1-3 years) effects, with information on long-term effects and the importance of fire for maintaining amphibian communities sparse for the majority of North American taxa (Pilliod et al. 2003, Gardner et al. 2007).

Amphibians should be particularly vulnerable to fire because they generally exhibit limited mobility and poor dispersal capabilities (relative to other vertebrates; Russell et al. 1999) and have moist permeable skin and eggs susceptible to desiccation (Stebbins and Cohen 1995). However amphibians also exhibit life history traits conducive to surviving direct fire effects including an aquatic life stage (for most species), affinity for moist locations, and subterranean and detrital habitat use (some species; Carpenter 1953, Jones et al. 2000, Pilliod et al. 2003). Some amphibians have apparently developed special sensory perceptions that allow them to detect approaching fire and seek refugia (Grafe et al. 2002). Thus, burning should not be viewed as equivocally detrimental to amphibian populations. In fact, the literature indicates that some amphibian species exhibit positive population responses to fire, mostly from the fire-induced perpetuation of critical habitat elements (Hossack and Corn 2007, also reviewed by Russell et al. 1999, Pilliod et al. 2003).

Fire obviously plays an important role in structuring amphibian terrestrial habitats (Jones et al. 2000, Oklahoma tallgrass prairie-oak forest), but research has shown that aquatic habitats are also sensitive to fire regimes (e.g., Bishop and Haas 2005, southeast United States). Canopy overgrowth in wetland ecosystems (like swamps, ephemeral pools, fens, or wet meadows) can cause localized amphibian population extinctions (Skelly et al. 1999, 2002), diversity loss (Werner and Glennemeier

1999, Werner et al. 2007), and reduced larval growth rates (Skelly et al. 2002). Although most research on the topic of wetland shading has occurred in forested environs, it follows that prairie-savanna amphibian species could potentially exhibit comparable responses to woody encroachment. Mechanisms for the observed amphibian responses include reduced dissolved oxygen, limited prey base, and decreases in water temperature (Skelly et al. 1999, Werner and Glennemeier 1999, Halverson et al. 2003).

No studies comparing amphibian population responses to different vegetation management techniques in the southern Great Lakes region were identified, though studies from outside the region suggest that fire is more detrimental to amphibian populations than grazing in prairie ecosystems, if the grazing regime is low intensity (Wilgers et al. 2006). Also, no studies were identified that quantified how amphibian populations respond to varying spatial and temporal fire regimes. Here again, research outside the region has indicated that landscape-level variables operating over multiple spatial and temporal scales influence amphibian population dynamics (Lehtinen et al. 1999). As such, fire regimes interact with variables like patch size, isolation, and seasonality and can significantly affect amphibian spatial dynamics (Lehtinen et al. 1999, Lehtinen and Galatowitsch 2001).

Some of the earliest research on the direct effects of fire on reptiles documented that temperatures in excess of 60 degrees C were lethal (rattlesnakes, Howard et al. 1959). Other studies have since demonstrated that intense fires result in snake mortality and changes in habitat use for the survivors (Erwin and Stasiak 1979, Means and Campbell 1981, Seigel 1986, Smith et al. 2001, Durbian 2006). Direct mortality seems to be related to ecdysis (shedding of external skin layers) that is hypothesized to decrease mobility and sensory perception (Rudolph et al. 1989). Some argue that fire-induced direct mortality among reptiles is offset by maintaining preferred or required habitat characteristics in fire maintained ecosystems (reviewed by Russell et al. 1999).

Reptiles tend to be more abundant on unburned areas, particularly in ecosystems that burn intensely (like prairies; Cavitt 2000, Jones et al. 2000), but this difference is often short-lived (Setser and Cavitt 2003). Factors contributing to the duration of fire effects on reptile communities include species mobility and presence of fire refugia (Setser and

Cavitt 2003). In fact, some reptilian species simply avoid fire by retreating into underground burrows (e.g., Louisiana pine snake, Rudolph et al. 1998; eastern massasauga, Durbian 2006). After the immediate direct effects of fire subside, reptile populations in prairie-savanna ecosystems can respond favorably (Brodman et al. 2002). In some instances, fire-maintained habitats are crucial for population persistence and genetic diversity (e.g., Templeton et al. 2001).

RESEARCH NEEDS

Amphibians and Reptiles

- Studies to examine how amphibian life states are impacted by fire, due to effects on aquatic, riparian, and upland habitats to address landscape scale (Gardner et al. 2007) and population –level (Pilliod et al. 2003) response
- Surveys that last for more than one year, and careful evaluation of historical data to estimate changes in range or population declines (Skelly et al. 2003) in areas managed with prescribed fire
- Evaluation of the the combined effects of the frequency, intensity, and seasonality of prescribed fires on herps (Russell et al. 1999)

Birds

Species-specific responses by birds to fire in prairie-savanna ecosystems vary greatly. For example, Henslow's sparrows (*Ammodramus henslowii*) seem to avoid burned habitats (Herkert 1994, Walk and Warner 2000) whereas bobolinks (*Dolichonyx oryzivorus*) (Herkert 1994) and upland sandpipers (*Bartramia longicauda*) (Powell 2006) are attracted to burned areas. These species-specific responses are determined by post-fire habitat structures and burn frequency, with avian species requiring grasses and shrubs (e.g., grasshopper sparrow [*Ammodramus savannarum*], Henslow's sparrow, dickcissel [*Spiza americana*], eastern meadowlark [*Sturnella magna*], Bell's vireo [*Vireo bellii*]) decreasing in abundance the season after a

fire whereas those ground-nesting species requiring sparse vegetation (e.g., upland sandpiper) increase in abundance (southern Indiana, Aquilani et al. 2000; southern Ohio, Artman et al. 2001; Kansas tallgrass prairie, Powell 2006). A similar habitat-based gradient in avian abundances was observed by Brawn (2006) in remnant Illinois savannas that were periodically burned. Those species requiring dense tree canopies or shrubby understories (e.g., red-eyed vireo [*Vireo olivaceus*], wood thrush [*Hylocichla mustelina*], veery [*Catharus fuscescens*], ovenbird [*Seiurus aurocapilla*], scarlet tanager [*Piranga olivacea*]) were selected against whereas those associated with more open canopies and herbaceous dominated ground layers (mourning dove [*Zenaida macroura*], red-headed woodpecker [*Melanerpes erythrocephalus*], indigo bunting [*Passerina cyanea*]) were positively affected by management (Brawn 2006, also see Davis et al. 2000 for similar results). In general, frequent prescribed fire tends to reduce insectivorous bird species that feed in shrubs or in the upper tree canopy while increase omnivorous species (that feed on ground and lower in tree canopies) and insectivorous bark gleaners (Davis et al. 2000).

While frequent fire appears to maintain habitat structure that is important for some avian species, the specificity of those species and how they utilize the habitat is not clear. Hartung and Brawn (2005) found that restoration status of oak savanna influences bird habitat use and foraging ecology. Results from Davis et al. (2000) suggested that up to 20 bird species are associated with frequently burned areas. However, few bird species are uniquely concentrated in oak savannas and woodlands, with the possible exception of red-headed woodpeckers (Brawn 2006, Grundel and Pavlovic 2007). Research suggests that frequent fire is often related to increased abundance of some declining bird species (Davis et al. 2000, Grundel and Pavlovic 2007), even if avian species are not targeted in the management plan (see Wood et al. 2011 for effects of Karner blue butterfly management on avian community). Some birds (eastern wood-pewee [*Contopus virens*], red-eyed vireo, black-capped chickadee [*Poecile atricapillus*], Baltimore oriole [*Icterus galbula*]) used oak trees in proportion to their availability in fire-maintained, open canopy savannas but specifically selected for oak in fire-excluded, closed canopy savannas (Hartung and Brawn 2005). Species-specific responses to burn

regimes emphasize the importance of landscape-level habitat heterogeneity (in both space and time) to avian populations (Best 1979, Davis et al. 2000, Fuhlendorf et al. 2006).

Few studies have evaluated how fire influences nesting and avian population demographics. Brawn (2006) found that daily bird nest survival rates (nesting from the ground to the tree canopy) were greater on restored savanna for species that were abundant across habitat types, but Aquilani et al. (2000) found lower nest success on burned oak forests in southern Indiana. Artman and Downhower (2003) noted that wood thrushes nesting in southern Ohio oak forests continued to nest in burned areas but that nest site selection behaviors changed. Nesting shifted to unburned patches that still retained live shrubs and saplings. Artman and Downhower (2003) detected no significant difference in nest success between burned and unburned wood thrushes. Other researchers similarly failed to detect a fire effect on bird pair bonding or mate fidelity and actually documented lower rates of nest desertion and parasitism after burning (Best 1979).

Nest parasitism has been linked to fire with both positive and negative effects. For example, Davis et al. (2000) showed an increase in brown-headed cowbird (*Molothrus ater*) abundance following prescribed fire, consistent with a concern addressed by Robinson (1994) that restoration of savanna ecosystems with fire potentially exacerbates the cowbird problem. Increases in cowbird abundance undoubtedly relate to landscape context and not solely to fire activity. Research has shown that populations of brown-headed cowbirds tend to associate with agricultural areas (e.g., Rodewald and Yahner 2001) and thus, restoration sites that occur in a matrix of agriculture are likely candidates for cowbird parasitism. These results further enforce the importance of understanding landscape context when describing faunal response to fire and other disturbance events.

The use of non-fire disturbances (e.g., grazing, mowing) alone or in combination with fire are also likely to influence avian community response. For example, some differences in bird species occurrence have been documented in grazed plant communities dominated by warm- and cool-season grasses (Walk and Warner 2000). Also, patch-burn grazing did not produce the expected habitat heterogeneity or avian community response

expected when applied in tallgrass prairie sites in Iowa and Missouri (Pillsbury et al. 2011). Mowing or haying may also impact birds. Although timing mowing activities around peak nesting activities may reduce the negative impacts on grassland birds (Brennan and Kuvlesky 2005), reliance upon mechanical vegetation manipulation is unlikely to attain desired avifauna objectives, as some species seem particularly dependent on the vegetation community structure that results from fire (e.g., red-headed woodpecker; King et al. 2007).

Avian population responses to management regime are area- and landscape-context sensitive. In fact some studies have observed that surrounding landscape characteristics have a more significant influence on animal community structure than the individual treated patches (Tester 1989, Wood et al. 2011). Researchers studying birds in disturbance-mediated landscapes have noted that associated avifauna is area-insensitive (Hunter et al. 2001, Brawn et al. 2002, Brawn 2006). This pattern seems especially true for small treated areas (e.g., 3-10 ha; Brawn et al. 2002, Van Dyke et al. 2004), or if the treated patches occur in a matrix of alternate or substitute habitats (Wood et al. 2011). However, small treatments will exclude certain species (Herkert 1994). As treated areas increase in size, patch area becomes increasingly important for describing avian population responses to burning (Herkert 1994, Artman et al. 2001). It has also been suggested that overall avian community abundance decreases after larger-scale (10's of ha) burns (Walk and Warner 2000). This suggests that both size of the area burned and quality of adjacent habitats are important considerations in managing prairie and oak savanna remnants for avian species.

RESEARCH NEEDS

Birds

- Effects of prescribed fire as compared to grazing, patch-burn grazing, or mowing on avian community response (Walk and Warner 2000, Pillsbury et al. 2011)
- Impact of size prescribed fires on avian communities (Artman et al. 2001)

Mammals

Although mammals are vulnerable to fire (e.g., Crowner and Barrett 1979), most population responses are attributed to habitat changes as opposed to direct mortality (Krefting and Ahlgren 1974, Dubis et al. 1988). Mammalian population responses are species-specific and depend on the interaction of fire intensity with litter layer thickness, habitat affinities for dense vegetation and foliage, nest location (above or below ground), and locomotion ability (Kaufman et al. 1990, Converse et al. 2006). There is substantial information on how fire affects mammal populations (primarily small mammals; reviewed by Bendell 1974), but few studies have occurred in the southern Great Lakes region. Small mammals are especially vulnerable to ring fires that offer few escape routes (Harty et al. 1991). Data from a Minnesota oak-savanna burn dominated by a dense mat of Kentucky bluegrass (conducted in late April) found that soil temperatures did not exceed 59 degrees C (late April) suggesting that those small mammals seeking subterranean refuge were not exposed to lethal temperatures (Tester 1965).

One species of particular concern in this region is the Indiana bat (*Myotis sodalist*). These tree roosting bats are endangered, and prescribed fires may have negative impacts if conducted when adult bats are hibernating or pups are at the age where they cannot fly and are too large to be carried (Dickinson et al. 2009). While the impacts of fire on bats in the southern Great Lakes region are not well studied, evidence from mixed hardwood forests in Kentucky suggest the impacts may be limited (Dickinson et al. 2009, Lacki et al. 2009). Northern bats (*Myotis septentrionalis*) monitored before, during, and after prescribed fires were observed to change roosts, in some cases while there was active fire (Dickinson et al. 2009), but otherwise were not obviously negatively impacted (Lacki et al. 2009). Additionally, models of heat and gas in smoke plumes suggest that low intensity fires (flame length <1.6m) may be unlikely to do physical damage, since bats tend to roost above the height where temperatures that can cause tissue damage are sustained in low intensity fires (Dickinson et al. 2010).

Post-burn vegetation structure and composition are important determinants of mammal population responses (Beck and Vogl 1972, Dubis et al. 1988, Kaufman et al. 1990, Converse et al. 2006). Small

mammals can rapidly recolonize burned areas if some habitat elements remain (e.g., Tester 1965), though recolonization rates depend on species (e.g., voles (4 months) may colonize faster than shrews (19 months)) and juxtaposition of unburned areas (see review in Kaufman et al. 1990, Harty et al. 1991). Poor population performance on burned areas is usually attributed to short-term forage and cover reductions that negatively influence fecundity and survival (Crown and Barrett 1979). Although some negative fire effects have been documented on mammals (e.g., Dubis et al. 1988, Harty et al. 1991), researchers have also demonstrated the importance of maintaining herbaceous dominated prairie-savanna ecosystems (i.e., limit woody encroachment) to support small mammal populations (Beck and Vogl 1972, Converse et al. 2006). Research also indicates that browsers may preferentially use burned areas, presumably because of increased palatability and forage access (Vogl and Beck 1970).

No studies in the southern Great Lakes region compared mammal population responses to burning versus other vegetation management approaches. A study encompassing multiple United States geographies by Converse et al. (2006) found few statistically significant differences in effect sizes among thinning, fire, and thinning-fire combination treatments on small mammal populations.

RESEARCH NEEDS

Mammals

- Effects of prescribed burn on endemic faunal communities in general, specifically related to frequency and seasonality of fire
- Impacts of prescribed fire on tree roosting bats (Dickinson et al. 2009)

CONCLUSIONS

Less extensive research on the effects of prescribed fire in prairie-savanna ecosystems in the southern Great Lakes region has been published when compared to other grassland and savanna communities (e.g., western tallgrass prairie, longleaf pine savanna). The majority of southern Great Lakes studies are specific to sites and/or species and few studies generalize their findings to the region. The literature indicates that prescribed fire is a useful tool for managing the vegetation of prairie and savanna ecosystems and maintaining habitat for some wildlife species of concern. Numerous studies demonstrated that prescribed fire in the southern Great Lakes region increase diversity of herbaceous species but questions as to the optimal season and frequency of prescribed fire application remain. Further, a common management suggestion in the fire literature is the importance of leaving unburned refugia on the landscape, as a way to improve the chances of escape and recolonization of flora and fauna in isolated patches.

This review highlights the complexities of using fire to manage the plants and animals found in prairie and savanna ecosystems. Fire effects are influenced by drought, topography, vegetation composition, grazing, mechanical management techniques, and other factors (Anderson 1990), and these factors often interact to influence outcomes. While these specific effects complicate making general statements about how a site will respond to a single prescribed burn, it is important to recognize that site specific factors should be considered when planning for prescribed fires. Additionally, managers should explicitly prioritize their management outcomes and design prescribed fire programs to accomplish those priority objectives, recognizing that tradeoffs in species responses will occur. Land managers, fire practitioners, and plant or animal ecologists should negotiate and align their burn objectives with ecological objectives supported by research and monitoring (e.g., Cook 2000).

It is important to note that although this review was fairly extensive, it is likely to have overlooked less available reports and documents examining prescribed burning across the southern Great Lakes region. However, we believe that this review offers a reasonable representation of the existing published literature on the subject for the defined area. Similarly, the research needs highlighted in each section do not represent the full extent of research needs on topics related to prescribed fire in the region.

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